BRILL

ETHNOGRAPHIC EVIDENCE FOR THE PRESENCE OF THE COCONUT CRAB BIRGUS LATRO (LINNAEUS, 1767) (ANOMURA, COENOBITIDAE) ON FLORES ISLAND, INDONESIA

Author(s): GREGORY FORTH

Source: *Crustaceana*, 2019, Vol. 92, No. 8 (2019), pp. 921-941

Published by: Brill

Stable URL: https://www.jstor.org/stable/10.2307/26784528

REFERENCES
Linked references are available on JSTOR for this article:
https://www.jstor.org/stable/10.2307/26784528?seq=1&cid=pdf-reference#references_tab_contents
You may need to log in to JSTOR to access the linked references.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms

Brill is collaborating with JSTOR to digitize, preserve and extend access to *Crustaceana*

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

BRILL

Crustaceana 92 (8) 921-941

CRUSTACEANA

ETHNOGRAPHIC EVIDENCE FOR THE PRESENCE OF THE COCONUT CRAB *BIRGUS LATRO* (LINNAEUS, 1767) (ANOMURA, COENOBITIDAE) ON FLORES ISLAND, INDONESIA

BY

GREGORY FORTH[1])
Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada T6G 2H4

ABSTRACT

Although occurring elsewhere in Indonesia, the coconut crab — the only member of the genus *Birgus* — has yet to be documented on the island of Flores or adjacent islands in the Lesser Sundas. In the Lio region of Flores, however, people in the district of Mego describe a very large entirely terrestrial crab occasionally encountered between 2 and 7 km from Flores' south coast and sometimes even further inland. Ethnographic evidence is presented showing how this crab, locally called 'kepi', generally corresponds to the coconut crab in regard to morphology, habitat, and behaviour. Because local people prohibit the killing and consumption of kepi, other factors possibly accounting for the reputed rarity of large land crabs possibly corresponding to *Birgus* are also discussed, and the case is further used to comment on the value of local knowledge for international zoology.

RÉSUMÉ

Bien que présent ailleurs en Indonésie, le crabe des cocotiers — le seul membre du genre *Birgus* — nécessite encore d'être documenté sur l'île de Flores ou les îles voisines dans les petites îles de la Sonde. Dans le pays Lio de l'île de Flores, cependant, des habitants du district de Mego décrivent un très grand crabe terrestre rencontré occasionnellement à l'intérieur de l'île, entre 2 et 7 km de la côte Sud et quelquefois même plus. L'évidence ethnographique est présentée en montrant comment ce crabe, appelé localement 'kepi', correspond généralement au crabe des cocotiers en considérant sa morphologie, son habitat, et son comportement. Etant donné que les populations locales interdisent de tuer et de consommer le kepi, d'autres facteurs possibles expliquant la rareté reconnue des grands crabes terrestres correspondant peut-être à *Birgus* sont aussi discutés ; ce cas est aussi utilisé pour commenter la valeur du savoir local pour la zoologie internationale.

INTRODUCTION

In the Mego district, in the far eastern part of the Lio ethno-linguistic region on the Indonesian island of Flores, people report very occasional sightings of

[1]) e-mail: gforth@ualberta.ca

© Koninklijke Brill NV, Leiden, 2019

DOI 10.1163/15685403-00003912

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

very large crabs that do not live in water, unlike marine and freshwater crabs which they encounter more regularly and with which they are thus more familiar. Local accounts describe the crabs not only as creatures of the dry land but as occurring in highland forests on this mountainous island, and usually in places several kilometres from the sea. Combined with their rarity, the phenomenon of a large terrestrial crab living out of water and far from the sea has given rise to a supernatural representation of the creatures as manifestations of capricious and dangerous forest spirits and therefore as fearful things to be avoided. For the same reason, local people deem it taboo ('pire') to injure, kill, or consume such a crab. With the exception of familiar supralittoral crabs called 'koa', whose flesh is described as very bitter and even poisonous, all other kinds of crabs known to Flores people, both marine and freshwater species, are caught and eaten regularly.

Mego people call the giant crabs 'kepi' (with the /e/ pronounced approximately as the /u/ in English 'guppy'), and it is by this name that I shall continue to refer to them. Owing to their supernatural representation, as manifestations of spirits that can mystically cause illness or death even to a person who simply and accidentally encounters them, it might be supposed that kepi are imaginary creatures or at best a gross exaggeration based on smaller, more common crabs. In fact, in Lio villages to the west of Mego, the name 'kepi' is applied instead to large marine bivalves, and these are similarly claimed to appear occasionally on dry land in highland forests, where they present a spiritual danger identical to that which Mego people attribute to the large crabs. Kepi of this sort, Lio further claim, are especially dangerous when they open and close their shells, as living marine shellfish are also known to do. It is beyond question that large terrestrial bivalves are imaginary; they are most likely explained by occasional findings, mentioned by Lio, of large sea shells, on or near the surface, in locations well away from the sea. By contrast, Mego accounts of the form, size, and behaviour of the crabs they name kepi provide strong evidence of encounters with specimens of *Birgus latro* (Linnaeus, 1767), the coconut crab also known as the robber crab, a large terrestrial crustacean which occurs on islands in the Indian Ocean, ranging eastward through the Indonesian archipelago to the western Pacific.

The purpose of this article is to detail indigenous knowledge of large forest crabs named kepi in order to show how it corresponds with documentation of *Birgus* by scientific zoologists. This correspondence also facilitates commentary on the value of local, or folk zoological, knowledge for scientific zoology. In all parts of Flores for which I have information, the crabs are either considered rare or are entirely unknown. In fact, the only place outside of the Lio region where I heard of large terrestrial crabs possibly corresponding to *Birgus* was the Sikkanese ethnolinguistic region, where a resident of the district of Néle mentioned the singular appearance of a large 'sea crab' some years previously, at a location 6 km

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

from Flores' north coast. By contrast, on smaller islands in the Indian and Pacific oceans *Birgus* is relatively common or was so until recently, the species' current scarcity being attributed to harvesting of the crabs for consumption or sale in most parts of its known range. In 1981 the coconut crab was listed as 'vulnerable' on the IUCN Red List. In 1996 this was changed to 'data deficient', but more recently the species has been described as 'rapidly declining' (Drew et al., 2010: 46), with predation by humans identified as the main cause. Particularly as Mego and other Lio people prohibit the killing and eating of land crabs corresponding to *Birgus*, therefore, I also discuss the possible demographic status of the crabs on Flores and factors that might account for their putative rarity.

THE DISTRIBUTION OF *BIRGUS LATRO* IN INDONESIA

There appear to be no zoological reports confirming the presence of *Birgus* on Flores, an island of the southern hemisphere (8.6574°S, 121.0794°E). Some distribution maps appear to show Flores falling within the crab's range (see, e.g., Lavery & Fielder, 1991: 87), but these are small-scale and generally undetailed, and the earliest published map (in Reyne, 1938) shows a hiatus between islands in the Indian Ocean — to the west of Java and Sumatra, where coconut crabs have also not been reported — and islands of the Pacific. Similarly, a more detailed map published in Monk et al. (1997: 596, fig. 8-6) shows the 'former range' of coconut crabs in eastern Indonesia as including only northern Sulawesi and adjacent islands and the whole of the Moluccan Islands.

Although the precise geographical source of his knowledge is not specified, what may be the first European report of *Birgus latro* in Indonesia dates to the sixteenth century, and derives from the Portuguese navigator António Galvão (Jacobs, 1971: 69), who described the crabs' diet as comprising coconuts and 'kenari' nuts (*Canarium* sp.). In the early eighteenth century, Rumphius (1999 [1705]: 27) gave a more detailed description of coconut crabs on Ambon and neighbouring islands of the Moluccas. A comprehensive review of reports from the nineteenth and early twentieth centuries pertaining to the distribution of *Birgus* in Indonesia is contained in two papers by Reyne (1938, 1939). In these, Reyne documents the presence of the crab in Menado (or Manado, on the north coast of Sulawesi), on the Moluccan islands of Ambon (Amboyna), Halmahera, Talaud, Ternate, Tidore, Buru, Seram (Ceram), and in the Kei, Tanimbar, and Aru islands of the southern Moluccas. But in the eastern Lesser Sundas, which besides Flores include the islands of Sumba and Sumbawa, these studies show *Birgus* as being present only in eastern Timor (now the new nation of Timor Leste) and smaller islands (e.g., Kisar) immediately to the north (Reyne, 1938: 242-44).

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

More recent studies confirm the continuing presence of *Birgus* in the Moluccas and the Sulawesi region; locations include Naira (Banda Islands, Haig & Ball, 1988); Manado (in north Sulawesi, Hamasaki et al., 2015); the Nanusa Islands (off northern Sulawesi, Reppie, 2015), Ternate and west Halmahera Island (in the northern Moluccas, Serosero et al., 2016), south and north Halmahera (Serosero et al., 2018); and the Liwo and Sayasi Islands (northern Moluccas, Widiyanti et al., 2015, 2016). There is no indication that extant populations do not still occur in other Indonesian regions identified by Reyne (1938, 1939). But whatever their current status in the latter locations, the survival of the crabs in Sulawesi and the Moluccas alone makes the occurrence of *Birgus* on Flores not only possible but probable. Because these almost entirely terrestrial crabs must nevertheless deposit their eggs in the sea, where the larvae can be carried considerable distances before infant crabs emerge onto dry land, the main reason is the 'Indonesian Throughflow', a series of currents originating in the southwest Pacific, which proceed southward along the west side of Sulawesi and from there into the Flores Sea, immediately to the north of Flores Island, as well as into the Banda Sea and from there into the Savu Sea, to the south of Flores (Sprintall et al., 2009). Both the north and south coasts of Flores would therefore appear to fall within the range of *Birgus* larval dispersal.

Whether larvae carried south from Sulawesi or the Moluccas was ever sufficient to establish a breeding population on Flores is another question. Nevertheless, ocean currents linking Flores with these more northerly islands, evidently the centre of *Birgus latro* in Indonesia, could certainly facilitate transitory populations on Flores, which because of the species' long lifespan (recently calculated as more than 100 years, Drew et al., 2013) could survive for decades if not centuries before further replenishment from the Moluccas or Sulawesi. In addition, Flores is a long and narrow island, and Mego lies not far west of its narrowest north to south point, a distance of some 13 km. Also because the area between this point and southern Mego is relatively flat, and not broken by any major mountain chain, it seem possible, in view of the considerable distances *Birgus* can range inland, that crabs developing from larvae deposited on Flores' north coast could find their way to the south.

According to Hartnoll (1988a: 16) almost all records of *Birgus* are from small islands. With an area of some 14 300 km^2, Flores is hardly small, but then neither are Sulawesi and Timor — not to mention New Guinea, Madagascar, and Taiwan and the former occurrence of the coconut crab on large land masses, including northeastern Australia (Reyne, 1938). There are no ecological and biogeographical grounds for believing that the species does not occur on Flores or did not do so formerly, so for this reason as well the species' occurrence on the island should not be surprising. In addition, since the disappearance or reduction of populations in

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

attested locations appears to be primarily anthropogenic, the fact that local people taboo the crabs they call kepi, prohibiting not only their killing but cultivation and settlement at locations where specimens are encountered, provides another reason why *Birgus*, assuming this is the zoological reference of the Mego category, might be expected to survive on Flores.

THE COCONUT CRAB, MEGO PEOPLE, AND MEGO TERRITORY

An overview of *Birgus latro*

Named 'coconut crab' owing to the long disputed claim (Reyne, 1939) that the creature can climb coconut palms to feed on the nuts, *Birgus* is the largest of the world's terrestrial arthropods. Upper size limits vary from source to source and employ different measures, but include a carapace width reaching 200 mm (thus approximately 78 mm in thoracic length; Drew et al., 2010: 46) and a leg span (length from the tip of one leg to the tip of the opposite leg) of nearly one metre (Reese, 1987: 196; Monk et al., 1997: 597). Citing various reports from different locations, Reyne (1939: 307) similarly mentions a 'span of [the] feet' of 76 cm and figures of 38 to 46 cm and 50 cm from the top of the chelae to the end of the abdomen. But by any measure, this is a large crustacean, and weighing up to 4 kg (Drew et al., 2010: 56) also a heavy one.

Reaching maturity at five years, the coconut crab is air-breathing (what gills it has are vestigial) and among the 'most fully terrestrial' of the world's crabs (Hartnoll, 1988a: 46). After mating on land, only the females revisit the ocean, in order to spawn. The larvae then emerge from the sea after 23 to 30 days, when they enter mollusc shells like the smaller hermit crabs to which the coconut crab is related, but these they discard entirely after three to four weeks (Wolcott, 1988: 87). Like most terrestrial animals, the coconut crab requires fresh water mainly for drinking, although a relatively cool, moist environment is necessary to prevent desiccation, especially when moulting; and for these reasons, the crabs prefer shady, forested areas and occupy earthen burrows or crevices in rocks. As noted by Drew et al. (2010: 57), during the moult terrestrial crabs like *Birgus* are 'exceptionally vulnerable to predation and desiccation' and 'minimise this vulnerability by moulting in shallow burrows'. In most of their range, coconut crabs are also generally nocturnal, emerging to search for food around dusk. Yet their degree of nocturnalism varies according to the presence of diurnal predators, most notably humans, and in some places they move about and feed during the daytime (Rumpff, 1986: 93; Brown & Fielder, 1991: 5).

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

Ethnographic and geographic setting

Like other Lio, Mego people are mostly cultivators or fishermen. They speak a dialect that has been classified as 'eastern Lio', by contrast to their neighbours immediately to the west who mostly speak 'central Lio' (Suryati et al., 2013). This dialectal contrast coincides with the previously mentioned use of the name 'kepi' to refer, on the one hand, to a large terrestrial crab and, on the other, to a large marine shellfish. My research was concentrated in southern parts of Mego, including settlements on Flores' south coast. Like Lio in general, the entire region is largely mountainous, though in some places narrow coastal plains intervene between uplands and the shore. Although forests have been reduced since the beginning of the colonial era in the early twentieth century, forested areas occur throughout southern and central Mego and rainfall is sufficient to maintain a generally green landscape, even during the dry season. In regard to the possible occurrence of *Birgus* in this region, it should be noted how on Christmas Island, which has the world's largest and apparently best studied population of coconut crabs, the species inhabits 'a multitude of vegetation types ranging from open coconut lined beaches through to dense tropic rainforest areas on plateaus over 300 m above sea level' (Drew et al., 2010: 50; cf. Rumpff, 1986: 24-27).

For a large part, the indigenous domain of Mego coincides with the modern 'sub-district' (Indonesian 'kecamatan') of the same name, with an area 111.26 km^2 and a population (in 2018) of 12 592. The southernmost part of this territory, bordering on the Savu Sea, is dominated by 'Mount Bhéra' (Kéli Bhéra), a peak some 800 m in elevation. Formerly swidden cultivation was practised on Mount Bhéra, but since people moved to lower lying settlements in the late twentieth century, this is now much reduced and in consequence the peak is more continuously forested than in times past. My enquiries were centred in the village of Léke Ba'i (8.71°S 112.08°E), which now serves as the capital of the administrative district named Mego, but were further conducted in numerous other Mego villages as well as in several settlements to the west of Mego. Unfortunately, I never had the opportunity to enquire about large terrestrial crabs in Lio communities on Flores' north coast, part of whose territory falls within the traditional domain of Mego. However, being much drier and far less continuously forested than the south coast and the mountainous interior, which can receive over 2000 mm of rain per year, the north coastal region would appear to provide a less suitable habitat for *Birgus*. As noted by Drew et al. (2010: 50, cf. Rumpff, 1986: 93-96, 103), on Christmas Island the population density of coconut crabs is highest in areas with the highest humidity (with the drier terraces of the northern third of the island only sparsely populated).

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

METHODS

Ethnographic evidence on kepi was generated by a combination of directive and non-directive questioning and derives from 29 informants, all except one of whom were men. Information was recorded first in 2016 but mostly in 2017 and 2018, when I spent a total of seven weeks in the Lio region. Of the 29 informants, 14 had seen a kepi on at least one occasion. Two eye-witnesses had seen kepi twice, in both instances in two different places and many years apart; thus in total there are 16 sighting accounts. In all but 4 instances, the person was alone at the time of the sighting. All reported sightings were by men. One woman had seen a kepi while in the company of her husband, but since I did not question her separately and because she merely confirmed what her husband had told me, I do not count her as a separate witness. Although many women have heard about kepi, they appear generally to have less experience of the crabs, largely because women's activities do not involve them spending nearly as much time in forest and other places outside of villages as do men's. Eye-witnesses were shown a black-and-white photograph of *Birgus latro*, and although some seemed more positive than others, all agreed that the photograph corresponded to what they saw. The photograph, however, was always shown after informants had described the object of their sightings, and in all instances responses to the photo were complementary rather than crucial to informant accounts.

My informant sample was non-random. After opportunistically collecting general descriptions of kepi, I mostly sought out older men who were most likely to have encountered a kepi at some time in their lives, and many of these were identified by asking others about people who might have experience of kepi (or what has been called 'snowball sampling'). These aspects of the methodology explain why as many as 14, thus nearly half, of a total of 29 informants claimed to have seen a kepi, a proportion that might otherwise appear to qualify the creature's reputed rarity. All but eight of the 29 informants who described kepi resided in the Mego region. Two men, both of whom had seen such a crab, were from Mbengu, a partly coastal region immediately to the west of Mego. Another three were residents of the administrative settlement (Indonesian 'desa') named Léna-Nda Réta, to the northwest of Mbengu, and yet another three were from Watu Néso, even further to the west. None of the last six claimed ever to have seen a kepi.

GENERAL KNOWLEDGE OF KEPI IN MEGO

Mego people regard kepi as a peculiar kind of crab with a distinct place in their folk taxonomy. The most general term for 'crab' is 'kojo', which implicitly labels a category comprising both marine crabs ('kojo mesi', or 'sea kojo') and freshwater

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

crabs (‘kojo ae’ or synonymous ‘kojo lowo’, ‘river kojo’). Insofar as Lio equate ‘kojo’ with Indonesian ‘kepiting’, a general term for ‘crab’, the folk taxon further encompasses: (1) ‘mango’, large marine crabs larger than ‘sea kojo’; (2) ‘koa’, crabs found close to the shore where they burrow in sandy soil; (3) ‘mbongga’, a very small kind of freshwater crab found in high mountain streams, which is primarily contrasted to larger freshwater kojo (kojo ae); and (4) a similarly small sort of crab called ‘keri kembi’ typically found at the edge of water courses but also described as capable, like kepi, of climbing on rocks and even some way up trees. A fisherman in the coastal village of Ma’u Lo’o (in the Mbengu region) said keri kembe occur on beaches as well as near fresh water. As my ethnographic project allowed neither the time nor resources to identify these crabs scientifically, I am unable to associate them with Latinate binomials. Informants described keri kembe, a semi-aquatic or riparian crab, as reddish or dark in colour with red on the limbs (‘kembe’ denotes a tree used in the manufacture of a red dye). But although this colouring and the tree-climbing habit might suggest immature specimens of *Birgus latro*, everyone I asked insisted that kepi and keri kembe were distinct kinds. Another crab or crab-like creature separately named by Mego is ‘kuma’, which inhabits beaches. The Mego description (including the creature’s entering shells and periodically discarding these to enter another) strongly indicate a hermit crab (see also Proto-Austronesian and Proto-Malayo-Polynesian *qumang, ‘hermit crab’, Blust, 2002: 131).

As a category of Mego folk taxonomy, kepi contrasts with kojo (equated with Indonesian kepiting, ‘crab’) in the most inclusive sense. People thus often describe kepi as ‘resembling’ or ‘having the form of’ kojo, and (when speaking Indonesian) as ‘looking like a crab (kepiting)’, yet from other statements about kepi it is quite clear that they regard kepi as a kind of crab. How much the contrast of kojo and kepi owes to the belief that kepi are manifestations of forest spirits, a representation not applied to other crabs, is difficult to determine. For Mego, however, kepi are different from other crabs on morphological and behavioural grounds. Apart from their great size — as large or larger than marine crabs called ‘mango’ — their peculiarity, as commonly articulated by Lio, is that unlike virtually all other crabs, they do not live in water, either fresh or salt water. As this was further expressed, whereas other large crabs (kojo mesi and mango) are normally found in the sea while smaller crabs inhabit bodies of fresh water, kepi are very large and yet appear in places far from rivers and streams, and even further from the sea. As an analysis of Lio cosmology would confirm, these sorts of inconsistency are connected in a particular way with their representation as supernatural creatures and as spiritually dangerous to humans.

As noted previously, in Lio dialects spoken to the west of Mego the name ‘kepi’ denotes not a crab but a large marine shellfish. Nevertheless, the term is

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

evidently related to Indonesian ‘kepit’, ‘pressed together, pinched’ (e.g., between two fingers; cf. ‘kepitan’, ‘clamp, pincers’), and moreover to Indonesian ‘kepiting’, ‘crab’, a name apparently focusing on a crab’s propensity to pinch. It might seem curious that, among the several Lio dialects and indeed throughout the larger group of Ngadha-Lio languages, ‘kepi’ seems to occur as the name of a crab only in the eastern Lio dialect spoken in Mego. On the other hand, the exclusive application of ‘kepi’ to a large terrestrial crab does not coincide with the distribution of such crabs, for I recorded similar reports of such creatures, including in some cases descriptions of them as supernaturally dangerous and therefore taboo, outside and to the west of Mego. The naming of crabs and shellfish as ‘kepi’ in different Lio dialects, it is worth noting, reflects the local view of both as creatures that are able to bite or pinch (in the latter case, by closing their shells). Among the linguistically related Nage of central Flores, well to the west of Lio, ‘kepi’ similarly names a kind of biting tick or mite that attaches itself to genital hair (Forth, 2016: 335, 347 n. 1). In Mego, an elderly spiritual practitioner further applied ‘kepi’, qualified as ‘kepi kéra’ (‘kéra’ is ‘turtle’), to rare and supernaturally powerful freshwater turtles (possibly *Cuora amboinensis* (Riche in Daudin, 1801), see Forth, 2018: 21), which are reputedly able to injure people by squeezing their fingers between the neck and carapace, while in another view, giant centipedes called ‘kipa kua’ (perhaps *Ethmostigmus rubripes* (Brandt, 1840)), which similarly deliver a nasty bite, should be counted as another kind of kepi.

As shown, general accounts by Mego focus on the very large size and peculiar, terrestrial habitat of kepi. More specifically, people describe them as living in ‘holes’ in the earth (i.e., burrows), sometimes in or near damp or marshy areas, but never in bodies of water. As commonly occurring in forest, kepi are further described as appearing near large trees and able to climb tree trunks (although informants thought never to the top). One specimen was found among the roots of a large tree that had been felled by wind, apparently the site of the crab’s burrow. Possibly referring to width from leg to leg, largest size estimates, offered by informants who themselves had never seen specimens, or at least none of this size, included ‘about 50 cm’, ‘larger than a frying pan’, and ‘the size of a rice winnow’ (that is, winnowing trays, typically of 45 to 50 cm in diameter). Also regularly mentioned is the rarity of kepi, often expressed by remarking how most people had never seen one or ‘will be able’ to see one. Of people who had never encountered a kepi, only one man mentioned the colour, which he described as ‘red’. Apart from the crabs’ large size and rarity, or the exceptional nature of their occurrence, people most commonly remark on the supernatural danger of encountering a kepi, including the risk of a person’s shadow falling on such a creature (which they claim, can result in death) and the taboo on cultivating or building settlements on land on which a kepi has been sighted.

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

SIGHTINGS

Information derived from the 16 eye-witness reports of kepi accord with the more general representation. These permit several generalizations.

Consistent with the solitary nature of *Birgus* (Dunham & Gilchrist, 1988: 137), a species that completes copulation quickly (Wolcott, 1988: 87) and whose females migrate to the sea primarily as individuals (C. Schiller et al., 1991), all kepi sightings were of single crabs. Twelve informants were able either to recall the year of a sighting or provide information from which the year could be estimated. The earliest sighting was in the early 1970s while the most recent was in August 2017. Seven of the 12 apparently took place after 2000, with 3 in the 2000s and 4 in the 2010s, whereas 2 were in the 1970s, 3 were in the 1990s, and none in the 1980s. Of course, from the fact that more sightings are reported from recent years, one cannot infer that the crab's numbers are stable, even less increasing, not only because of the memory factor but also because my informant sample was relatively small and non-random.

Seemingly contrary to the general nocturnalism attributed to *Birgus* (Hartnoll, 1988a: 18) all crabs were seen in daylight or around dawn, with no consistency in the hour of the sighting. On the other hand, an elderly man regarded as especially knowledgeable about kepi, or at least how to deal with them ritually, said the crabs usually appear around dusk (cf. Fletcher et al., 1991b: 65-66). However, depending on the presence or behaviour of predators, for some parts of its range *Birgus* has been described as sometimes diurnal (Brown & Fielder, 1991) or 'partially nocturnal' (Nokelainen et al., 2018), and the fact that no sighting took place after nightfall can simply be explained by the circumstance that, except for men hunting bats or other nocturnal prey, Lio do not normally travel at night through forested locations where the crabs are likely to be found, and by the fact that they never actively search for the crabs, which they therefore always encounter accidentally.

Eight informants were able to recall the time of year when they saw a kepi. Two sightings occurred in October, another in September or October, and another in October or November. The most recent sighting — in 2017, while I was present in the field but unfortunately not at the location where the crab appeared — took place in August. In another two cases, a kepi was described simply as being encountered in the 'dry season', in this part of Flores falling between April or May and October or November (heavy rain typically does not fall before December). Virtually all sightings were therefore remembered as occurring in the dry months, and most in the period between August and October. The only exception concerns one man who, questioned and re-questioned on different occasions, thought the crab he had seen, as long ago as the early 1970s, was encountered either in October or February (in the midst of the rainy season). That nearly all kepi sightings occurred during

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

the dry months could reflect the moulting behaviour of *Birgus*, since moulting crabs must remain hidden in burrows for some considerable time (3 to 16 weeks on Vanuatu, Fletcher et al., 1991a: 39) to allow the new shell to harden. Some authorities (e.g., Hartnoll, 1988b: 195) have described moulting in coconut crabs as occurring in the rainy season, and although Drew et al. (2010: 58) have provided contrary evidence, of coconut crabs in some places moulting during the dry season, moulting nevertheless appears to be seasonal in any given location. The evidence further suggests that mating also is seasonal, a factor that could more positively explain why crabs locally identified as kepi, presumably being more active and mobile at this time, are more likely to be seen during particular months. In addition, September and October are the time of year when people are preparing fields for planting (completed in late October or November) and clearing forest to make new fields, thus arguably providing more opportunities for coming across large forest-dwelling crabs.

Of the 16 sightings, six took place at locations 2 to 3 km from Flores' south coast. Four occurred at places 3.5 to 4.5 km from the south coast and another four at 5 to 7 km. Just two were more distant than this, being reported from locations over 9 km and 9.5 to 10 km from the nearest shore. With the possible exception of the last two, all these figures are consistent with published reports of *Birgus* occurring 'at the highest island elevations' (Burggren & McMahon (eds.), 1988: 383) and at distances of '6 km or more' from the sea on Christmas Island (Hartnoll, 1988a: 18).

Most sightings occurred outside of settlements and in forested areas. Locations described were near holes in the ground (assumed to be where kepi resided), under tree roots or otherwise near or below trees, on rocky ground, and inside water containers. Eye-witnesses and others sometimes spoke as though kepi regularly inhabit particular sites. This may reflect overgeneralization — a crab being seen at a certain spot and it then being inferred that it lives there or somewhere nearby — or the association of kepi with forest spirits, which are also believed to haunt specific locations, typically large trees or stones. On the other hand, the representation is consistent with information on site fidelity for the coconut crab reviewed by Drew et al. (2010: 52, 59). Three sightings took place at Ae Nine on Mount Bhéra, the location of a stream from which water is now conducted to lower-lying locations by way of a concrete tank and pipes. By contrast, in another three instances a crab appeared inside a village, and in another two inside a house. From the available literature (e.g., Dunham & Gilchrist, 1988), *Birgus* occurring in close proximity to humans seems not particularly unusual. Even so, it is of some interest that two of the sightings concerned crabs described as 'small' or 'very small' while in another case the size was not indicated. If these were not immature specimens of the coconut crab, then they would have been crabs of other species

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

that had somehow found their way into settlements. And if so, then rather than their form, it may have been the unusual occurrence of crabs in places where they do not normally occur that motivated their interpretation as kepi.

Among sightings occurring inside villages, one was the most recent (in August 2017), and the eye-witness account was among the most detailed. This was given by a male householder and confirmed by his wife, who had also seen the crab. In this case, the kepi — a relatively large specimen — was found inside a large metal drum containing drinking and bathing water; it had apparently entered by climbing about a metre up the accidented exterior wall of the house, against which the drum was placed. Since, as air-breathers, coconut crabs cannot remain submerged for long (McMahon& Burggren, 1988a: 292), this report may raise a question. However, the house-holders had first spotted the kepi inside the drum at about 9:00 am, after which they performed a simple ritual requesting the creature to leave. They then left to perform other tasks, and on returning some two hours later, discovered the crab was no longer in the drum. Thus if kepi are able to climb into large water containers, they are evidently able to climb out again, an observation that also applies to sightings of one such crab (described by two eye witnesses) inside a concrete tank at Ae Nine. And it is further consistent with descriptions, both by local people and by scientific zoologists (see Burggren & McMahon (eds.), 1988: 383; Nokelainen et al., 2018: 76), of coconut crabs as good climbers and, in the scientific literature, as using bodies of fresh water to drink.

If location and distance of kepi sightings are generally consistent with *Birgus*, then so too are eye-witness reports of their size, appearance, and behaviour. Whether informants' descriptions of size (length or width) referred to the body alone (carapace or thorax plus head) or to the combination of body and limbs (legs and chelae) was not always clear. Also, in most instances witnesses simply indicated size with their hands. Nevertheless, at least three estimates appeared to concern body size alone, and two informants specified the body, comparing this to the size of a coconut shell with the husk removed (about 10 to 15 cm, depending on variety). On the other hand, the largest estimates (respectively 30, 35, and 40 cm) could have referred to leg span, though even if the reference were just to the body, or to a combination of the body and head (cephalothoracic length), the largest crab was still within the upper limit reported for *Birgus*.

Nine of the 16 sighting reports of kepi allowed a numerical estimate of size. Of these, 3 were 30-40 cm, 4 were around 25 cm, and 2 were 10-15 cm. In addition, of the 7 reports where there was no clear estimation of size, one informant described the crab as large. Another two spoke of a specimen as small or very small, and another as small or 'average', but all these specifications were relative to kepi in general or possibly to large or the largest kepi the eye-witnesses had heard about. As thoracic length at maturity appears to fall somewhere between

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

21 mm and 30 mm in *Birgus* (Drew et al., 2010: 57), the large majority of local sightings (assuming these were coconut crabs) apparently concerned mature and relatively large specimens. This generally large size might be a function of people not recognizing smaller crabs, whatever their species, as kepi. But probably a more likely explanation is that it reflects the cryptic behaviour of immature coconut crabs, as well as the low rate of recruitment of juveniles (deriving from eggs deposited in the sea) back to terrestrial parent populations (Drew et al., 2010: 49-50, 60). Referring to evidence from Vanuatu, Brown et al. (1991: 91) suggest that 'significant numbers of [coconut] crabs may recruit only every five to ten years'. In addition, estimates of the crabs living longer than 100 years (Drew et al., 2013), a life span that would allow them to reach a considerable size, provide further support for the large terrestrial crabs Mego call kepi reflecting a population of *Birgus*.

Colours described by eye-witnesses also match the coconut crab, which occurs in two principal colour morphs labelled 'red' and 'blue', the latter sometimes described in the literature as 'black' (Nokelainen et al., 2018). The two morphs occur in single populations and are not linked with either size or sex. A brief note on Lio and Indonesian (Bahasa Indonesia) colour terminology is in order. Terms usually translated as 'black' ('mite', Indonesian 'hitam') can more generally mean 'dark' and can include dark browns, greys, and dark blues. Terms for 'red' ('méra', Indonesian 'merah') are further applied to dark orange and browns. And words for 'white' ('bhara', 'ja'; Indonesian 'putih') can encompass pale shades of a variety of hues, including pale yellow, pale pink, and pale blue. With these qualifications in mind, it may be noted that of 14 sighting accounts which mentioned colour, in five instances this was primarily or exclusively 'red' or 'reddish', in another case 'brown' (compared to a bag I carried), and in another 'greyish-brown' (Indonesian 'abu-abu'). Four mentioned 'black', though in one of these the colour was interrupted by brassy yellow marks or patches. Just one informant specified 'blue' (expressed with Indonesian 'biru') and this similarly concerned blue areas on an otherwise 'black' carapace and limbs. In addition, two crabs were described as 'white' or 'pale', though one of these also showed 'black' areas on the creature's back. Pallor could reflect specimens of *Birgus* that had recently moulted, when the new exoskeleton is pale bluish-white (Fletcher et al., 1991a: 41). As 'red' kepi were more common than kepi of other colours, it is noteworthy that the same disparity occurs in populations of coconut crabs. As Nokelainen et al. (2018: 85) observe with regard to an East African sample, blue adults (which formed a distinct minority) better match background near the shore. In fact, the only kepi described as largely blue was the one found closest to Flores' south coast. The location, however, was in an upland region some 2 km from the sea and so was hardly near

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

the shore. In three reports informants mentioned how the crab's underside was 'white', that is, lighter than the back.

Other features of kepi described by eye-witnesses included large front claws and long legs raising the crab high off the ground when walking. One man thus described the creature he saw as walking fast 'like a spider', and another observed that the crab, like kepi in general, walked (or 'glided') with its body raised above the ground rather than crawling on its belly, as he described other crabs doing. The same man, who on different occasions had seen two specimens and provided among the most detailed accounts, remarked how quickly one of the creatures was able to climb up a bank. Also corresponding to *Birgus*, a round or oval body was a feature mentioned by two eyewitnesses, with one describing the body as 'round' like the shell of a turtle rather than angular like those of other crabs. One man further described a kepi, apparently encountered at quite close range (he was squatting among trees to relieve himself at the time), as moving its two front limbs up and down, presumably in an agonistic display. Insofar as coconut crabs have been described as 'often display[ing] aggressive behaviours when confronted by humans' (Drew et al., 2010: 52; cf. Rumpff, 1986: 90-91), this too accords with *Birgus*.

Three observers mentioned protruding 'eyes' (eyestalks), with two specifying these as 'red' and one as having a length in extension of about 3 cm. Four people, including three eye-witnesses, described kepi as having 'hair', presumably referring to setae. According to two informants, this hair appeared on the claws (chelae) while the other two specified the legs, and one of the former two described the hair as not particularly stiff or straight but 'more like moss'. While describing the crab as otherwise dark ('black'), another man described the 'hair' as comprising several colours. Apparently speaking generally, a man who had encountered kepi on two separate occasions remarked that the 'skin' (carapace) was not as hard as that of other crabs, but this could have referred specifically to a pale crab he and two companions found in the roots of a fallen tree, which one of them prodded with a stick and which may have recently moulted.

No informant said anything about what kepi ate, how they mated or reproduced, or whether they produced sound. At the same time, whereas I often enquired specifically about size and colour, only twice did I explicitly ask about reproduction and diet, regarding which the informants said they did not know. In respect to sound, *Birgus* has been described as producing 'a continuous ticking sound' when not alarmed, and when approached, 'stamp[ing] sharply with one or both of the long second pereiopods' (Grubb, 1971: 412; see also Gibson-Hill, 1947: 51, who mentions 'a low, chittering sound'). In view of the association of coconut crabs with coconuts, including their apparent ability to remove husks and break shells to consume the flesh (Reyne, 1939; Drew et al., 2010), it should also be noted that no one

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

I spoke to ever mentioned coconuts in connection with kepi, even though the palms are cultivated throughout Flores. But then I never specifically enquired about this either. The coconut crab is by no means dependent on coconuts anywhere in its range, and in fact the species consumes a variety of plant and animal foods (either killed or as carrion), including the fruit of *Pandanus* (screwpine), *Ficus* (fig), and *Canarium* trees and jackfruit *Artocarpus integer* (Thunb.) Merr. (also quoted under the synonymous name *Artocarpus integrifolius* L. f.; Drew et al., 2010: 53), all of which are available in the Lio region.

DISCUSSION

For the most part Lio statements about the form and behaviour of crabs Mego people call kepi correspond to *Birgus latro* and are therefore indicative of a continuing presence of this species on Flores Island. Especially in view of the locations of kepi sightings and details of the creature's size, morphology, and habits, it is unlikely that local reports reflect encounters with crabs of other species. Flores appears to fall within the range of another land crab, *Cardisoma carnifex* (Herbst, 1796). However, this species is much smaller than *Birgus* (see Burggren & McMahon (eds.), 1988: 383-384), is supralittoral rather than terrestrial (Cameron, 1981), and is 'the most closely mangrove-associated land crab species' (Tomasic et al., 1997: 982) and so does not range far from the sea. As a species that breathes partly through gills, for which reason it has been described as 'amphibious' rather than 'terrestrial' (McMahon & Burggren, 1988a: 290), *C. carnifex* also requires regular immersion and thus never occurs far from bodies of water and, while on land, inhabits deep, partly water-filled burrows. In addition, if *C. carnifex* does occur in Lio territory, in view of its habits the crab is likely to be better known than *Birgus*, or the creature called kepi, and may even be one referent of the name 'koa', a category of crustacean that has none of the supernatural aura of kepi, the primary factor in Lio interest in these large, terrestrial, forest-dwelling crabs.

The reputed rarity of kepi — a local perception essential to their supernatural representation as creatures of the sea that occasionally appear on dry land where, in the local view, they definitely do not belong — raises questions about the present status of a hypothetical population of *Birgus latro*. On most Indian Ocean and Pacific islands where coconut crabs occur, they are hunted and consumed; indeed, unexploited populations appear to be relatively few (Drew et al., 2010: 49), and human exploitation has been identified as the biggest threat to the species' survival (Wolcott, 1988: 91; Brown et al., 1991: 99). In Mego, by contrast, harming or killing kepi (or what the evidence suggests are *Birgus*) is strictly taboo, and although some traditional taboos are now no longer observed, with just one

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

exception I never heard of anyone deliberately killing such a crab. The exception was a woman from Sulawesi (whom I was never able to meet), the wife of a Mego man, who was reputed to have killed and cooked a crab identified as a kepi that appeared inside her house — an action that amazed and repelled her Mego neighbours. Also qualifying the exception, the crab was described as small and thus less certainly a specimen of *Birgus* than were the objects of other sightings. Interestingly, two men in the region of Watu Néso, some 15 km to the west of Mego, separately mentioned the former presence of large forest-dwelling crabs, in this region not called kepi nor known by any special name, which people once hunted and consumed but which disappeared locally, perhaps three to four decades ago. The crabs were described as occurring far from the sea, living in 'holes' (burrows up to 10 cm in diameter, according to one account), and in other ways corresponding to *Birgus*. But if such crabs were once exploited, indeed annually hunted during a 'certain season' as one man suggested, then in this region they were apparently not deemed taboo as they are in Mego.

If human exploitation cannot account for the reputed rarity of a hypothetical population of *Birgus latro* in Mego, it is worth considering other factors that could. That killing or capture by humans is not the sole reason for recent population decline in coconut crabs elsewhere, is indicated by a study of *Birgus latro* on Sayafi Island in the Moluccas, where the population has been declining although the exploitation rate of this crab has not been optimal (Widiyanti et al., 2016: 159-160). For Flores at least, one factor could be deforestation (cf. Brown et al., 1991: 101), the cutting of trees for timber and the clearing of land for fields and human habitation. As Rumpff (1986: 111) notes for Christmas Island, while numerous elsewhere, coconut crabs were almost completely absent in areas where forest had been cleared for mining or human settlement. Another factor is predation by non-humans. For Vanuatu, Fletcher et al. (1991a: 54) identify pigs as possible predators, 'able to locate moulting crabs in burrows by smell and dig them up'. On Flores, if not domestic pigs (which for some time have been kept penned by government order), then still plentiful wild pigs could be a significant predator, and since wild pigs are largely nocturnal, this could be another reason — in addition to absence of exploitation by humans — why a Flores population of *Birgus* might be more active during the day. On the other hand, if such crabs were partly or largely nocturnal, this would be another reason why people would seldom encounter them and thus consider the creatures in general to be rare.

It has also been suggested that small coconut crabs are eaten by larger crabs of other species, as well as by large toads, monitor lizards, birds and rats (Nokelainen et al., 2018). Except for large toads, all these animals occur in Lio. At the same time, I never heard of any of them feeding on kepi — nor indeed of pigs or any other animal doing so. In some places nocturnal rats have been proposed as a

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

danger to coconut crabs and, on Christmas Island, specifically as a cause of diurnal behaviour (Drew et al., 2010: 51). As the world's largest murid, the endemic Flores giant rat *Papagomys armandvillei* (Jentink, 1892), a primarily nocturnal animal, might seem an especial threat to any coconut crabs that may occur on Flores. Yet despite the danger these sharp-toothed, largely arboreal rodents pose to hunters and their dogs (Forth, 2016: 120-121), unlike other rat species the giant rat is locally described as entirely herbivorous, though Musser (1981: 130) has speculated it may eat some insects as well.

Factors that would definitely limit the survival of *Birgus* on Flores are therefore equivocal at best, and a more likely explanation for the local perception of the crabs as rare is that their numbers are indeed small. As suggested earlier, specimens that may occur might not represent an established breeding population. Rather, they could reflect a small number of crabs resulting from low extrinsic recruitment from islands to the north, which given the coconut crab's remarkable longevity, could be sustained for long periods, especially as human predation does not limit population size.

According to Reyne (1939), local people's knowledge of *Birgus* is reliable only when it concerns locating and capturing the crabs and preparing them for consumption. Mego people, however, do not capture and consume kepi; in fact they explicitly prohibit their killing and yet are able to provide sufficient information on the morphology and behaviour of these crabs to reveal a substantial correspondence with *Birgus latro*. Reyne's view reflects a long-standing attitude of utilitarianism, which assumes that folk knowledge of biota (including folk taxonomy and nomenclature) is fundamentally grounded in practical uses people make of natural species. Yet detailed studies of folk zoology in specific ethnolinguistic communities (e.g., Forth, 2016) have refuted this claim, revealing that people other than professional scientists often possess a good deal of empirically valid information about animals that have no economic or other practical use whatsoever. Lio knowledge of kepi crabs prospectively provides another case in point. And while the broader debate may appear to be of interest mainly to anthropologists, local knowledge of kepi points to a relevance for biologists as well, for it shows how various kinds of local knowledge, not all of them associated with economic values, can contribute to biological research into species like *Birgus latro*, which are either in decline or approaching extinction.

Reported by both Galvão (Jacobs, 1971: 69) and Rumphius (1999 [1705]: 27), the coconut crab's ability to feed on coconuts has been contested for some 300 years. This controversy too bears in an interesting way on the value of local knowledge for biologists, for as Reyne (1939) has documented at length, many accounts of the crabs consuming coconuts ultimately derive from local people, and partly for this reason have been disputed by Western writers, including Reyne

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

himself. Apart from claims that the crabs are able to climb to the tops of coconut palms, dislodge the nuts, and then descend to the ground where they open them and consume the flesh, a particular doubt concerns the coconut crab's ability to open 'uninjured' nuts (Reyne, 1939: 298) — that is, fresh nuts with the husk and shell intact — with its claws. More recently, however, Rumpff (1986: 72-73) and others have recorded large coconut crabs feeding on unripe as well as ripe nuts and as being able to open ripe, undamaged coconuts, although according to Drew et al. (2010: 53) the process is often lengthy 'and may involve many individuals before access to the coconut is acquired'. Once again, then, research by scientific zoologists has eventually confirmed the validity of knowledge of natural species possessed by local people that Western observers earlier regarded as fantastic, fanciful, or at any rate, unlikely (see also Forth, 2017: 304).

Clearly, only zoological investigation of crab populations on Flores can confirm the presence and present status of the coconut crab on that island. Still, in regard to size, morphology, and behaviour, *Birgus latro* is so different from other land crabs found in this part of Indonesia as to significantly limit the possibility of confusion with other species (R. G. Hartnoll, pers. comm. 2019). Therefore, the close correspondence of local descriptions of kepi with details of *Birgus* establishes beyond reasonable doubt the probable presence of this species on Flores and by the same token justifies future field research.

ACKNOWLEDGEMENTS

Research in the Lio region was funded from an Insight Grant awarded by the Social Sciences and Humanities Research Council of Canada. Although I am naturally grateful to all of them, local people who participated are too numerous to mention. Nevertheless, I would like to extend special thanks to Venantius ('Venan') Bhara and his family who generously hosted me in the their house in Léke Ba'i, and Wenseslaus Dago, Venan's elder brother, who first told me about kepi and in many other ways assisted my ethnographic enquiries. Thanks are also due to Richard Hartnoll of Liverpool University, who offered several observations about the distribution of *Birgus* in Indonesia that he has kindly allowed me to incorporate in a revision of the present paper.

REFERENCES

ARNDT, P., 1933. Li'onesisch-Deutsches Wörterbuch. (Arnoldus-Druckerei, Ende-Flores).

BROWN, I. W. & D. R. FIELDER, 1991. Project overview and literature survey. In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph, **8**: 1-11. (Australian Centre for International Agricultural Research, Canberra).

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

BROWN, I. W., D. R. FIELDER & W. J. FLETCHER, 1991. Conclusions. In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph, **8**: 99-102. (Australian Centre for International Agricultural Research, Canberra).

BURGGREN, W. W. & B. R. MCMAHON (eds.), 1988. Biology of the land crabs: i-xii, 1-479. (Cambridge University Press, Cambridge).

BURGGREN, W. W. & B. R. MCMAHON, 1988a. Biology of the land crabs: an introduction. In: W. W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 1-5. (Cambridge University Press, Cambridge).

BURGGREN, W. W. & B. R. MCMAHON, 1988b. Circulation. In: W. W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 298-332. (Cambridge University Press, Cambridge).

CAMERON, J. N., 1981. Brief introduction to the land crabs of the Palau Islands: stages in the transition to air breathing. Journal of Experimental Zoology, **218**: 1-5.

DREW, M. M., S. HARZSCH, M. STENSMYR, S. ERLAND & B. S. HANSSON, 2010. A review of the biology and ecology of the robber crab, *Birgus latro* (Linnaeus, 1769) (Anomura: Coenobitidae). Zoologischer Anzeiger, **249**: 45-67.

DREW, M. M., M. J. SMITH & B. S. HANSSON, 2013. Factors influencing growth of giant terrestrial robber crab *Birgus latro* (Anomura: Coenobitidae) on Christmas Island. Aquatic Biology, **19**: 129-141.

DUNHAM, D. W. & S. L. GILCHRIST, 1988. Behavior. In: W. W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 97-138. (Cambridge University Press, Cambridge).

FLETCHER, W. J., I. W. BROWN, D. R. FIELDER & A. OBED, 1991a. Moulting and growth characteristics. In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph, **8**: 35-60. (Australian Centre for International Agricultural Research, Canberra).

FLETCHER, W. J., I. W. BROWN, D. R. FIELDER & A. OBED, 1991b. Structure and dynamics of populations. In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph, **8**: 61-86. (Australian Centre for International Agricultural Research, Canberra).

FORTH, G., 2016. Why the porcupine is not a bird: explorations in the folk zoology of an eastern Indonesian people: i-xiv, 1-375. (University of Toronto Press, Toronto).

FORTH, G., 2017. Ethnographic reports of freshwater turtles on Flores Island: the possibilities of an undocumented chelonian species. Herpetological Review, **48**(2): 304-310.

FORTH, G., 2018. Further evidence for undocumented freshwater turtles on Flores Island, Indonesia. Herpetological Review, **49**(1): 19-21.

GIBSON-HILL, C. A., 1947. Christmas Island — terrestrial crabs: field notes on the terrestrial crabs. Bulletin of the Raffles Museum, **18**: 43-52.

GRUBB, P., 1971. Ecology of terrestrial decapod crustaceans on Aldabra. Philosophical Transactions of the Royal Society of London, (B) **260**: 411-416.

HAIG, J. & E. BALL, 1988. Hermit crabs from north Australian and eastern Indonesian waters (Crustacea Decapoda: Anomura: Paguroidea) collected during the 1975 *Alpha Helix* expedition. Records of the Australian Museum, **40**: 151-196.

HAMASAKI, K., C. IIZUKA, A. OJIMA, M. SUGIZAKI, A. SUGIMOTO, S. DAN & S. KITADA, 2015. Genetic diversity and demographic history of the terrestrial hermit crabs *Birgus latro* and *Coenobita brevimanus* in the north-western Pacific region. Journal of Crustacean Biology, **35**: 793-803.

HARTNOLL, R. G., 1988a. Evolution, systematics, and geographical distribution. In: W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 6-54. (Cambridge University Press, Cambridge).

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

HARTNOLL, R. G., 1988b. Growth and molting. In: W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 186-210. (Cambridge University Press, Cambridge).

JACOBS, H. TH. TH. M. (ed. and translator), 1971. A treatise on the Moluccas (c. 1544): probably the preliminary version of Antonio Galvão's lost História das Moluccas. Sources and Studies for the History of the Jesuits, **3**. (Jesuit Historical Institute, Rome).

LAVERY, S. & D. R. FIELDER, 1991. Genetic characteristics. In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph, **8**: 87-98. (Australian Centre for International Agricultural Research, Canberra).

MCMAHON, B. R. & W. W. BURGGREN, 1988a. Respiration. In: W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 249-297. (Cambridge University Press, Cambridge).

MCMAHON, B. R. & W. W. BURGGREN, 1988b. Epilogue. In: W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 378-381. (Cambridge University Press, Cambridge).

MONK, K., Y. DE FRETES & G. REKSODIHARJO-LILLEY, 1997. The ecology of Nusa Tenggara and Maluku. The Ecology of Indonesia Series, **5**: i-xvii, 1-966. (Periplus Editions, Hong Kong).

MUSSER, G. G., 1981. The giant rat of Flores and its relatives east of Borneo and Bali. Bulletin of the American Museum of Natural History, **169**: 71-175.

NOKELAINEN, O., M. STEVENS & T. CARO, 2018. Colour polymorphism in the coconut crab (*Birgus latro*). Evolutionary Ecology, **32**: 75-88.

REESE, E. S., 1987. Terrestrial environments and ecology of Enewetak Atoll. In: D. M. DEVANEY, ET AL. (eds.), The natural history of Enewetak Atoll, **1**. The ecosystem: environments, biotas, and processes: 187-202. (U.S. Department of Energy, Office of Scientific and Technical Information, Oak Ridge, Tennessee).

REPPIE, E., 2015. Local wisdom *mane'e* and its impact on fish resources and environment in Nanusa Islands, North Sulawesi, Indonesia. Journal of Biodiversity and Environmental Sciences, **6**: 156-161.

REYNE, A., 1938. On the distribution of *Birgus latro* L. in the Dutch East Indies. Archives Néerlandaises de Zoologie, **3**(2-3): 239-247.

REYNE, A., 1939. On the food habits of the coconut crab (*Birgus latro* L.) with notes on its distribution. Archives Néerlandaises de Zoologie, **3**(2-3): 283-320.

RUMPFF, H., 1986. Freilanduntersuchungen zur Ethologie, Ökologie und Populationsbiologie des Palmendiebes, *Birgus latro* L. (Paguridea, Crustacea, Decapoda) auf Christmas Island (Indischer Ozean). [Ethology, ecology, and population biology field studies of the coconut crab, *Birgus latro* L. (Paguridea, Crustacea, Decapoda) on Christmas Island (Indian Ocean)]. (Doctoral Thesis, Westfälische Wilhelms-Universität, Münster, Germany).

RUMPHIUS, G. E., 1999 [1705]. The Ambonese curiosity cabinet. Translated, edited, annotated and with an introduction by E. M. BEEKMAN: i-cxii, 1-567. (Yale University Press, New Haven and London).

SCHILLER, C., D. R. FIELDER, I. W. BROWN & A. OBED, 1991. Reproduction, early life-history and recruitment. In: I. W. BROWN & D. R. FIELDER (eds.), The coconut crab: aspects of *Birgus latro* biology and ecology in Vanuatu. ACIAR Monograph, **8**: 13-34. (Australian Centre for International Agricultural Research, Canberra).

SEROSERO, R. H., SULISTIONO, N. A. BUTET & E. RIANI, 2018. Morphometric characteristics of coconut crabs (*Birgus latro* Linnaeus, 1767) in North Moluccas Province, Indonesia. Bioflux, **11**: 1616-1632.

SEROSERO, R. H., SURYANI & RINA, 2016. Karakteristik habitat dan pola pertumbuhan kepiting kelapa (*Birgus latro*) di Pulau Ternate dan Kabupaten Halmahera Barat Provinsi Maluku Utara: habitat characteristics and growth pattern of coconut crab (*Birgus latro*) in Ternate Island and West Halmahera, North Maluku Province. Depik, **5**: 48-56.

SPRINTALL, J., S. E. WIJFFELS, R. MOLCARD & I. JAYA, 2009. Direct estimates of the Indonesian Throughflow entering the Indian Ocean: 2004-2006. Journal of Geophysical Research, **114**: 1-9.

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms

SURYATI, M., A. M. MBETE, M. LAUDER & M. DHANAWATY, 2013. Phonological and lexical varieties of Lio language in Flores, East Nusa Tenggara: A study of geographical dialect. e-Journal of Linguistics, **6**: 1-27.

TOMASCIK, T., A. J. MAH, A. MONTJI & M. K. MOOSA, 1997. The ecology of the Indonesian seas, part II. (Periplus Editions, Hong Kong).

WIDIYANTI, S. E., MARSOEDI, SUKOSO & D. SETYOHADI, 2015. Resource management of coconut crab (*Birgus latro*) in Liwo island, North Maluku of Indonesia. Journal of Biodiversity and Environmental Sciences, **6**: 343-351.

WIDIYANTI, S. E., MARSOEDI, SUKOSO & D. SETYOHADI, 2016. Population dynamic of coconut crab (*Birgus latro*) in Sayafi Island, North Maluku of Indonesia. Journal of Biodiversity and Environmental Sciences, **8**(6): 151-161.

WOLCOTT, T. G., 1988. Ecology. In: W. W. BURGGREN & B. R. MCMAHON (eds.), Biology of the land crabs: 55-96. (Cambridge University Press, Cambridge).

First received 25 January 2019.
Final version accepted 23 April 2019.

This content downloaded from
76.24.71.246 on Sat, 28 Mar 2026 03:03:15 UTC
All use subject to https://about.jstor.org/terms